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Susceptibility of wheat to mildew as influenced by carbohydrate supply

SAM F. TRELEASE AND HELEN M. TRELEASE

Although the significant features in the nature of the host plant that determine its degree of susceptibility to disease are as yet very imperfectly understood, recent studies have shown that susceptibility of plants to parasitic disease may be profoundly influenced by environmental conditions, of temperature, moisture, light, mineral nutrient supply, etc. And in some cases valuable suggestions have been obtained regarding the manner in which the effective internal conditions of the host may be influenced. For a number of plant diseases caused by obligate parasites a general correlation exists in many cases between host vigor and susceptibility to disease—the more vigorous host being more susceptible to such diseases than the less vigorous host (Raines, 1922). Carbohydrate nutrition, in particular, has been found to have an important influence on the degree of susceptibility of the host to rusts and to mildews.

Fromme (1913) reported tests on the effect of light exclusion on the development of *Puccinia coronifera* on oats. Four cultures of the same age, seven days, were inoculated. One was placed in a darkroom and the other three were put in the greenhouse, in a glass box. After three days the first culture was transferred from the darkroom to the greenhouse. The incubation period for the three cultures kept in the greenhouse was eight days, while that of the culture left three days in the darkroom was eleven days. The difference of three days in the incubation period was exactly equal to the period of light exclusion and indicated a complete arrest of the development of the fungus in the darkroom. In another experiment, the effect of light exclusion during the latter part of the incubation period was tested. Four cultures were inoculated and placed in the greenhouse, in the glass box. Four days later one of them was transferred to the darkroom, where it was left four days, and then returned to the culture box. No signs of infection were visible on this culture at this time,

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while unripe pustules on the other cultures were plainly visible. The pustules on the cultures that remained in the greenhouse ripened on the ninth day, while three additional days, twelve days in all, were necessary for a similar development of the culture that had been in the darkroom. By excluding light four days in the latter part of the normal incubation period, maturation of the rust had been delayed three days. Thus, even after the fungus had become well established in the host, its development was strongly retarded in complete darkness. Fromme says that the retardation of the growth of the fungus may be the direct effect of total absence of light on the fungus itself. Or it is possible that the fungus simply suffers from lack of food, since the host is incapable of photosynthesis in darkness. He suggests, however, that it seems hardly possible that such a complete inhibition in the growth of the fungus should have resulted in the brief time involved unless the fungus is dependent on the transition products of photosynthesis. This latter possibility, he states, is by no means inconceivable, and should this explanation prove the correct one it could be made the basis for an explanation of the obligate parasitism of the rusts and their inability to develop on any form of artificial medium.

Reed (1914) studied the influence of light on infection of wheat and barley by mildews. Seedlings were grown in the dark until the first leaf was 2–3 cm. long and then inoculated with mildew spores from their respective hosts. Some of the inoculated plants were kept continuously in the dark and some were removed at once and placed in the light; at intervals of 24 hours other inoculated plants were transferred to the light. The general results were that no infection occurred if the plants were kept in the dark after inoculation. After removal of the seedlings to the light, infection occurred in proportion to the degree to which the etiolated leaves turned green. In general the period of incubation was retarded proportionally to the time the plants were kept in the dark. Another series of experiments was carried out, first growing the plants in the light and then, after inoculation, placing them in the dark, some immediately, others after intervals of 24 hours. In the case of the plants placed at once in the dark, no infection occurred. Those, however, that were kept in the

light for one or two days became infected. The period of incubation of the fungus, however, was materially retarded. Reed emphasizes the importance of chlorophyll, since he states that in general the effect of absence of light upon the mildew is considered to be an indirect one and has to do with the primary effect upon the development of chlorophyll in the host cell. The infection fails to occur, he says, in those cells which have not developed the chlorophyll. The mildew, according to Reed, is a strict parasite, not attacking cells which are not capable of carrying on their normal functions. These results, he says, are quite different from those obtained by inoculating etiolated plants with saprophytic fungi; under such conditions, in some cases at least, saprophytic fungi are able to develop on the living tissues.

Mains (1917) has reported experiments on the effects of light and carbohydrate supply upon the development of *Puccinia Sorghi* on maize and *Puccinia coronata* on oats. He found that when leaves or seedlings were first deprived of carbohydrates, light was necessary for the development of these parasites on their hosts since it is necessary for the formation of carbohydrate by the hosts. When the host was able to obtain a supply of carbohydrates from a solution, light was not necessary for the development of either parasite. The development of *Puccinia Sorghi* was checked when the host was deprived of carbon dioxide. Pure cultures of *Puccinia Sorghi* were maintained upon sterile seedlings and upon pieces of maize leaf floated upon solutions of starch, sucrose, dextrose, maltose, and dextrin in the dark. Development of the fungus did not occur unless a carbohydrate was present in the solution. Mains considers that the obligate parasitism of the rusts may probably be explained by their requirement of some transitory or nascent organic products, related to the carbohydrates, which they secure in the living host.

Leach (1919) has used specific food requirements of fungi as the basis of an hypothesis to explain the phenomena of rust resistance and biologic specialization in rusts. He considers that each biologic form of rust requires a specific food, which is produced only in a limited number of host forms.

The study here reported was planned in order to obtain

further information concerning the effect which carbohydrate supply might have upon the susceptibility of the host to parasitic disease. Wheat mildew was selected as representing a disease that could be readily studied under greenhouse and laboratory conditions.

INFLUENCE OF LIGHT UPON SUSCEPTIBILITY

Effect of period in dark after inoculation upon incubation period. The data recorded in table 1 were obtained in tests made to determine the effect of the length of an initial period in darkness upon the incubation period of wheat plants inoculated with mildew (*Erysiphe graminis*). Seedlings of Leap's Prolific (winter) wheat were grown in a shaded greenhouse for seventeen days in four-inch pots, about fifty seedlings in a pot. The seedlings, which were about 18 cm. high and had two expanded leaves, were sprayed with distilled water and inoculated at 5 o'clock in the afternoon with mildew spores shaken from heavily infected plants. Three similar tests were made. In the first test inoculation occurred on July 26, 1927; in the second, on August 2, 1927; and in the third on June 11, 1928. In the third test the plants were kept in darkness for two days preceding inoculation, in order to allow exhaustion of surplus carbohydrate from the leaves.[1] For each test eight lots, as shown in table 1, of two pots each were used. Immediately after inoculation, the first lot was left in the greenhouse where it was exposed to the usual alternating periods of light and darkness; the others were placed in the dark, and one lot was removed to the greenhouse each day. The darkroom is adjacent to the greenhouse and receives a continuous supply of fresh air from the latter, by means of an electric fan; thus temperature (averaging about 25°C.) and humidity were nearly the same in the greenhouse and in the darkroom. Observations were made twice daily, at 9 A.M. and at 5 P.M.; and a record was obtained of the approximate time when spore tufts became visible on the leaves.

No development of mildew spores occurred on inoculated plants left for 7 days or longer in the dark; these plants were very chlorotic and died a few days after being placed in the

[1] Wheat leaves, even after exposure to bright light, appear to have only a small excess of carbohydrate food. See a later section of this paper.

greenhouse. After the plants had been in the dark for about 4 days, numerous light yellow flecks appeared on the leaves, indicating initial infection, but spore masses did not develop on these plants. The lack of susceptibility of wheat in the dark suggests at once, as was pointed out by Fromme (1913), Reed (1914), and Mains (1917), that the leaves are not susceptible unless they contain an adequate supply of carbohydrate foods, normally manufactured in the light by photosynthesis.

TABLE 1

Effect of period in dark after inoculation upon incubation period (time required for mildew appearance)[a]

PERIOD IN DARK, DAYS	INCUBATION PERIOD, DAYS				DELAY: INCUBATION PERIOD MINUS MINIMUM INCUBATION PERIOD, DAYS				PERIOD IN GREENHOUSE BEFORE MILDEW APPEARANCE, DAYS				PERIOD IN DARK MINUS DELAY, DAYS			
	1	2	3	Av.	1	2	3	Av.	1	2	3	Av.	1	2	3	Av.
0	3.5	4.0	3.0	3.5	0.0	0.0	0.0	0.0	3.5	4.0	3.0	3.5	0.0	0.0	0.0	0.0
1	3.5	4.5	3.5	3.8	0.0	0.5	0.5	0.3	2.5	3.5	2.5	2.8	1.0	0.5	0.5	0.7
2	4.0	4.5	3.5	4.0	0.5	0.5	0.5	0.5	2.0	2.5	1.5	2.0	1.5	1.5	1.5	1.5
3	5.0	5.0	4.0	4.7	0.5	1.0	1.0	0.8	2.0	2.0	1.0	1.7	2.5	2.0	2.0	2.2
4	5.5	5.5	5.0	5.3	2.0	1.5	2.0	1.8	1.5	1.5	1.0	1.3	2.0	2.5	2.0	2.2
5	6.5	6.5	7.0	6.7	3.0	2.5	4.0	3.2	1.5	1.5	2.0	1.6	2.0	2.5	1.0	1.8
6	7.5	8.5	8.0	8.0	4.0	4.5	5.0	4.5	1.5	2.5	2.0	2.0	2.0	1.5	1.0	1.5

[a] No infection occurred on plants left for 7 or 8 days in the dark; these plants were very chlorotic and died a few days after being placed in the light.

In the first test recorded in table 1 an initial period of 1 day in darkness did not lengthen the incubation period, but in the second and third tests it increased the incubation period by 0.5 day. Progressively longer periods in the dark definitely lengthened the incubation period. The delay in the appearance of mildew spores (actual incubation period minus minimum incubation period) varied directly with the length of the initial period in the dark.

The time required in the greenhouse before the appearance of mildew spores was less for the plants that had been in the dark than for those left in the greenhouse. Thus, tufts of mildew spores usually appeared in from 1.0 to 2.5 days after the plants were transferred from the darkroom to the greenhouse, whereas the minimum incubation period for plants remaining in the greenhouse was from 3.0 to 4.0 days. This indicates that

spore germination and some development of mycelium occurred in the dark. That absence of light did not completely arrest the development of the mildew is also shown by the last four columns of table 1. When the plants were kept in the dark for one or more days, the delay in mildew appearance was never as great as the period during which the plants had been in darkness.

Injurious effects of darkness and of mildew upon wheat. Some of the effects of mildew and of absence of light were observed after the plants were transferred from the darkroom to the greenhouse. These may be illustrated by a description of the appearance of the plants four days after the last culture had been removed from the darkroom. The plants were arranged in a series according to the length of their period in darkness, beginning with those that had not been in the darkroom after inoculation and ending with those that had remained for 8 days in the darkroom. This series represented progressively greater dwarfing, increased chlorosis, more pronounced drooping, and less abundant development of mildew. The plants which had been in the dark from 0 to 2 days were large and vigorous, dark green in color, erect, and heavily covered with tufts of mildew spores. Those which had been in darkness from 3 to 5 days were dwarfed (about three-fourths as tall as the preceding), increasingly chlorotic and wilted, and only sparsely covered with mildew conidia. And those which had been in the dark from 6 to 8 days showed greater dwarfing (being about one-half as tall as the plants not placed in the darkroom), they were extremely chlorotic, and they exhibited pronounced drooping. Only a very slight development of mildew spores was visible on the plants which had been in the dark for 6 days, and none on those which had been in darkness for 7 and 8 days.

Aside from showing the influence of darkness in rendering the plants less susceptible to mildew, these tests bring out the high degree of injury that results from exclusion of light. In fact, wheat plants seem to be injured more rapidly by darkness then by mildew. Seedlings are unable to survive a period of seven days in the dark, whereas they usually are able to live for two or three weeks with the most severe infection possible with mildew if other conditions are favorable.

These tests illustrate a difficulty met in attempting to correlate host vigor and susceptibility. The plants that were left in the greenhouse after inoculation were much more vigorous than those kept in the dark for 6 days, and, judging by their ability to support the fungus, they were much more susceptible to mildew. And yet the greater vigor of these plants enabled them to live considerably longer than the less susceptible plants that had been injured by lack of light. As time went on, the plants tended more and more to recover from the injury they sustained during the absence of light, but concurrently the injurious effects of the mildew infection became increasingly greater. Where two sets of adverse conditions have been operative together (here darkness and mildew infection), it may be difficult to evaluate the relative degree of injury that has been produced by either one of the conditions in question.

TABLE 2

Effect on mildew infection of placing inoculated plants in darkness after various initial periods in light[a]

INITIAL PERIOD IN LIGHT, DAYS	INCUBATION PERIOD, DAYS	
	PLANTS	CUT LEAVES[b]
0	[c]	[c]
1	[c]	[c]
2	3.5	3.0
3	3.0	3.0

[a] At beginning of test (June 24, 4 P.M.), the plants had been in the dark for 3 days; they were 12 days old, 19 cm. high.

[b] When potted plants were placed in the dark, six leaves were cut off and placed on wet blotting paper in a moist chamber.

[c] No infection occurred.

Effect on mildew infection of placing inoculated plants in darkness after various initial periods in light. Table 2 shows the results secured in a test made to determine the incubation period for plants that were inoculated and kept in the greenhouse for different periods of time and then transferred to the darkroom. The seedlings were grown in the greenhouse, and three days before inoculation they were put in the darkroom, so as to diminish the reserve carbohydrate food that they might contain. They were inoculated with mildew in the

greenhouse at 4 P.M. on June 24, 1928, when they were 12 days old and about 19 cm. high. The first set was placed immediately in the dark, the second was put in the dark after 1 day, the third after 2 days, and the fourth after 3 days. Duplicate pots, of about 50 seedlings each, were used for each treatment. When each set of plants was transferred to the dark, six leaves were cut off and placed on wet blotting paper in a moist chamber.

It will be seen from table 2 that no mildew developed on the plants placed immediately in the dark nor upon those left in the greenhouse for one day. But spores appeared after 3.5 days on the plants that remained in the greenhouse for 2 days before removal to darkness. This indicates that sufficient food—probably carbohydrate, protein, or both—was made or accumulated during the 2-day period to render the plants sufficiently susceptible to allow subsequent development of the parasite; secondary infection did not occur in the dark, however, and these plants died after about 12 days. The incubation period for mildew on the seedlings in the greenhouse was 3.0 days.

It is interesting to note that mildew spores may be formed sooner on cut leaves than on those remaining attached to the plant. This is seen in the case of the seedlings that had been in the greenhouse for 2 days before being transferred to the darkroom. The shorter incubation period was probably due to a greater retention of food by these leaf portions, since translocation was prevented by detachment from the basal growing region of the leaf as well as from the rest of the plant.

Slight development of mildew in dark on very young seedlings still receiving carbohydrate supply from endosperm. The tests thus far described were made with seedlings that had exhausted the carbohydrate of the endosperm and had been in darkness for a period of 2 or 3 days prior to inoculation (except in two tests recorded in table 1). In view of Mains's (1917) observation that the endosperm of maize continued for a long time to supply materials that allowed the development of rust in the dark, it seemed of interest to test the susceptibility of very young wheat seedlings that were still receiving food from the endosperm and had been carrying on

photosynthesis. For this purpose, seedlings that were only 4 days old, with the first green leaf about 8 cm. long, were inoculated at 4 P.M. on June 24, 1928, and placed immediately in the darkroom. At the end of four days a very slight development of small patches of mildew spores was visible on the leaves. Three days later, when the tufts had reached their maximum size, the amount of mildew was very small in comparison with the development on similar seedlings in the greenhouse.

Mildew development as an index of photosynthetic activity. The foregoing experiments, of course, suggest that the capacity of the wheat leaf to support the development of mildew might be used as an index of photosynthetic activity. This might prove useful for qualitative tests comparable to those of starch accumulation or increase in dry weight of the leaf.

INFLUENCE OF CARBOHYDRATE AND ALCOHOL SOLUTIONS UPON SUSCEPTIBILITY OF LEAVES IN DARKNESS

It has long been known that green leaves which have previously been freed from starch can absorb various organic substances from solution and form starch in the dark. The literature contains reports of many studies made to determine the species of plants in which starch formation may occur in darkness, the kinds and concentrations of organic substances that may be assimilated, and the effects of temperature and poisons on the process. Reference may be made here to the following workers who have made important investigations of these problems: Boehm (1883, 1889), Schimper (1885), E. Laurent (1886), Meyer (1886), Bokorny (1888), Acton (1889), Saposchnikoff (1889), Nadson (1890). Mazé (1899, 1911), J. Laurent (1904), Molliard (1907), Ravin (1913), Knudson (1916), and others have developed methods for growing green plants in sterile cultures and supplying them with organic substances through their roots.

Mains (1917) was able to grow pure cultures of *Puccinia Sorghi* upon sterile seedlings of maize and upon pieces of maize leaf floated upon solutions of starch, cane sugar, dextrose, maltose, and dextrin in the dark. The fungus did not develop upon either seedlings or pieces of maize leaf that

were exhausted of carbohydrates and supplied only with a salt solution or distilled water in the dark.

The foregoing studies suggested that wheat leaves kept in the dark might be susceptible to mildew if they were supplied with solutions of organic substances. Tests were therefore made to determine the effects of different kinds and concentrations of carbohydrate and alcohol solutions.

Effects of different kinds of carbohydrates and alcohols upon the development of mildew on wheat leaves in darkness. Seedlings of Leap's Prolific wheat were grown for fourteen days in four-inch pots, or until they were about 18 cm. high. After they had been placed in the dark for 2 days, to free them from a surplus of food, they were inoculated in the same manner as in the preceding tests. About 10 cc. of solution were poured into an ordinary Pyrex test-tube (150 mm. high and 18 mm. in diameter, without lip; capacity 30 cc.), and the test-tube was lightly plugged with absorbent cotton. The solutions were prepared with tap water, tests having shown that the development of the mildew was the same when tap water or distilled water was used. Three leaves were cut from the inoculated plants and quickly transferred to the test-tube. Each leaf portion, about 8 cm. long, floated in the solution, so that the cut end was submerged to a depth of about 2 cm. while the rest was exposed to the air within the test-tube. For each solution five test-tubes containing leaves were prepared and placed in the darkroom at an average temperature of about 21°C. The development of mildew on the leaves was observed by turning on an electric lamp for a few minutes, and final records were usually obtained after about seven days. No special precautions were taken to assure sterility of the preparations, but the mildew generally developed more rapidly than bacteria and other fungi, and the results were discarded where serious contamination occurred.

Table 3 shows the results secured with fourteen different carbohydrates and two alcohols. All of the solutions were prepared so as to have a carbon concentration equivalent to that of a 0.1 M dextrose solution. The various types of solutions differed in osmotic value, but the latter was never high enough to bring about injury to the leaves. Each of the fourteen carbohydrates and the two alcohols rendered the

leaves susceptible to mildew. Only a very few small spore tufts, hardly visible without the aid of a hand-lens, were formed on the control leaves supplied with tap water. Although exact estimation was not possible, the number of spores produced on the control leaves appeared to be less than one-hundredth as great as on the leaves marked in the table with a single *plus* sign.

TABLE 3

Development of mildew on leaves of wheat kept in darkness and supplied with solutions of carbohydrates and of alcohols; every solution prepared with tap water and equivalent in carbon concentration to a 0.1 M dextrose solution[a]

GENERAL CLASS	SUBSTANCE	DEVELOPMENT OF MILDEW
Monosaccharides	Arabinose [$C_5H_{10}O_5$]	+
	Xylose [$C_5H_{10}O_5$]	++
	Rhamnose [$C_6H_{12}O_5 \cdot H_2O$]	+
	Dextrose [$C_6H_{12}O_6 \cdot H_2O$]	+++
	Levulose [$C_6H_{12}O_6$]	+++
	Galactose [$C_6H_{12}O_6$]	++
	Mannose [$C_6H_{12}O_6$]	+
Disaccharides	Sucrose [$C_{12}H_{22}O_{11}$]	+++
	Maltose [$C_{12}H_{22}O_{11} \cdot H_2O$]	++
	Lactose [$C_{12}H_{22}O_{11} \cdot H_2O$]	++
Trisaccharides	Melezitose [$C_{18}H_{32}O_{16} \cdot 2H_2O$]	+++
Non-sugars	Starch [$(C_6H_{10}O_5)_n$]	+
	Dextrin [$(C_6H_{10}O_5)_n$]	+
	Inulin [$(C_6H_{10}O_5)_6 \cdot H_2O$]	+
Alcohols	Glycerine [$C_3H_5(OH)_3$]	++
	Mannite [$C_6H_8(OH)_6$]	+

[a] Only a few, extremely small tufts of spores developed on the control leaves, inoculated with mildew and supplied with tap water. Number of spores produced on these control leaves appeared to be less than one-hundredth as great as the number on leaves marked +.

The roughly quantitative comparison recorded in table 3 shows that the monosaccharides dextrose and levulose, the disaccharide sucrose, and the trisaccharide melezitose were most effective in increasing the susceptibility of the leaves to mildew. The monosaccharides xylose and galactose, the disaccharides maltose and lactose, and the alcohol glycerine

appeared to be less effective. And the monosaccharides arabinose, rhamnose, and mannose, the non-sugars starch, dextrin, and inulin, and the alcohol mannite seemed to be least effective. The reasons for these differences may be expected to depend upon a complex set of conditions, involving the rate of diffusion of the organic substance in question, the ability of the leaf cells to absorb the substance directly or after digestion by enzymes,[2] the rate of translocation of the substance or of its products from the subepidermal to the epidermal cells of the leaf, the capacity of the leaf cells to convert the substance into forms that can be used by the parasite, etc. The action of the organic substance may in some cases involve injurious chemical and osmotic effects upon host and parasite. Since the branched haustoria of the mildew penetrate only the epidermal cells (Smith, 1900), it is obvious that the growth of the fungus should be markedly influenced by the kinds and concentrations of substances within these cells.

All of the substances listed in table 3 are utilized by fungi and bacteria in artificial culture, and many of them induce the accumulation of starch in leaves supplied with them in darkness. By hydrolysis, of course, sucrose is converted into dextrose and levulose; maltose into dextrose; lactose into dextrose and galactose; melezitose into dextrose and turanose (isomeric with sucrose) and the latter into dextrose and levulose; starch into dextrin and maltose and the latter into glucose; and inulin into levulose. Little is known, however, concerning the nature of the chemical alterations which they undergo during utilization by fungi or by green leaves.

It is interesting to note in this connection that when leaves are supplied with sucrose solutions in the dark, there is an increase in the protein content of the leaves (Saposchnikoff, 1889, 1890, 1891, 1893), and proteins thus formed may be of importance in rendering wheat leaves susceptible to mildew. Although most fungi that can be grown in artificial culture are able to elaborate their own proteins from carbohydrates and simple mineral salts, sufficient evidence is not yet available to show how important a part the proteins of the host may

[2] It would be expected that absorption of colloidal starch could occur only after extracellular digestion, such as takes place in cultures of fungi or bacteria growing in starch media.

have in the development of obligate parasites. From present knowledge, it would not be safe to assume that the degree of susceptibility of wheat to mildew is simply a question of the kinds and concentrations of carbohydrates present in the wheat.

Fromme (1913), in attempting to explain the retardation of growth of oat rust on its host in the dark, suggests that the fungus may be dependent on the transition products of photosynthesis. The present tests indicate that mildew development may depend just as well upon products of digestion as upon products of photosynthesis. And it is apparent that many different carbohydrates, as well as glycerine and mannite, may furnish the wheat leaf with materials which, directly or indirectly, allow the fungus to derive nourishment.

The obligate parasitism of the rusts might be explained, according to Fromme (1913), by their dependence upon transition products in photosynthesis, or similarly, according to Mains (1917), by their requirement of some transitory or nascent organic products (certain stereoisomers, possibly) related to the carbohydrates, which they obtain only in the living host.

Specific food requirements of fungi have been found in many cases since Pasteur's original discovery of the action of *Penicillium glaucum* on dextro-, levo-, and racemic-tartaric acid.

Leach (1919) has elaborated an hypothesis to explain the phenomena of rust resistance and biologic specialization in rusts. He supposes that each biologic form of rust has its specific food requirements, conforming with the molecular configuration of its protoplasm. This food, which is in turn specific in relation to the protoplasm which produces it, is found only in a limited number of host species. When a given biologic form of rust invades a plant that does not contain this specific food, the fungus consequently dies of starvation and in this process of starvation secretes an enzyme that is injurious to the plant cells with which it comes in contact.

Experimental evidence is not yet available concerning the forms of food directly utilized by the rusts or by the mildews. It is clear, however, that the proper transformation of any one of many carbohydrates, as well as of glycerine and mannite,

occurs readily in the wheat leaf so that the required foods are supplied to the mildew. It is obvious, of course, that the reason why wheat is often susceptible to wheat mildew while barley is always immune to this fungus cannot be explained in terms of carbohydrate *content* (since both wheat and barley may have the same amount); but it might possibly be explained, as suggested by Leach, in terms of the *kind* of carbohydrate—no two plant species having exactly the same kind of starch, protein, etc.

TABLE 4

Development of mildew on leaves of wheat kept in dark and supplied with various concentrations of sucrose in tap water

CONCENTRATION		DEVELOPMENT OF MILDEW
Relative carbon concentration[a]	Grams per 100 cc. of solution	
0	0	0[b]
1/512	0.003	0[b]
1/256	0.007	0[b]
1/128	0.013	0[b]
1/64	0.027	0[b]
1/32	0.053	0[b]
1/16	0.107	0[b]
1/8	0.214	+
1/4	0.428	+
1/2	0.855	+
1	1.711	+++
2	3.422	++++
4	6.844	+++++
8	13.687	++++++
16	27.374	+++++++

[a] Ratio of carbon concentration to carbon concentration of a 0.1 M dextrose solution.

[b] Only a few, extremely small tufts of spores produced.

Effects of the concentration of sucrose, dextrose, and glycerine upon the development of mildew on wheat leaves in darkness. The results recorded in tables 4–6 were obtained in tests made to determine effects of different total concentrations of sucrose, dextrose, and glycerine upon the susceptibility of wheat leaves to mildew in darkness. In tables 4 and 5 the concentrations are expressed as relative values in which unity

represents a carbon concentration equivalent to that of a 0.1 M dextrose solution. In table 6 the concentrations are given in terms of osmotic value.

Only a few, extremely small tufts of mildew spores, generally visible only with the aid of a hand-lens, appeared on the leaves supplied with tap water alone. This development was so slight that it is recorded as zero in attempting to estimate the relative abundance of spores on the leaves (table 4). Relative concentrations of sucrose from 1/512 to 1/16 appeared to be no more effective in increasing the susceptibility of the leaves. But a clear increase in spore production was evident with relative concentrations of 1/8, 1/4, and 1/2; and increasingly higher concentrations gave greater development. The optimum concentration was not exceeded, since the highest concentration (16, or 27.374 grams of sucrose per 100 cc. of solution) allowed the most abundant production of spores.

In the tests recorded in table 5 an attempt was made to estimate more accurately the relative abundance of mildew that developed on leaves supplied with a series of concentrations of sucrose, dextrose, and glycerine. The preparation showing the greatest development of spores per unit leaf area was assigned a value of 100, and indices were given to the other preparations by comparison with this standard. Development of mildew in the tap water controls was extremely slight. With the sucrose solutions the abundance of mildew increased rapidly as the concentration became higher, and an optimum is indicated for a relative concentration of 16. Spore production on leaves supplied with the optimum solution was much more abundant than was ever observed on cultures in the greenhouse. Similar results were obtained with dextrose solutions. The lower concentrations of dextrose appeared to give somewhat higher values than the corresponding concentrations of sucrose, the optimum was reached at a lower carbon concentration than with sucrose, and a marked falling off in mildew development occurred with the highest concentrations. The lower concentrations of glycerine seemed to be more effective than similar concentrations of either sucrose or dextrose; the optimum was attained at a carbon concentration of only 4, and a rapid decrease in mildew is evident for concentrations exceeding

the optimum. At its optimum concentration glycerine was only about 50 per cent as effective as sucrose at its optimum, and dextrose was about the same as sucrose.

The data of table 5 have been rearranged in table 6 to bring out the relation of the osmotic concentration of the solutions to the development of mildew in the dark. Approximate osmotic values were calculated by the formula $\pi = MRT$, in

TABLE 5

Development of mildew on leaves of wheat kept in dark and supplied with various concentrations of sucrose, dextrose, and glycerine in tap water

RELATIVE CARBON CONCENTRATION[a]	DEVELOPMENT OF MILDEW		
	Sucrose	Dextrose	Glycerine
0	0[b]	0[b]	0[b]
1/32	1	1	1
1/16	1	1	1
1/8	1	1	2
1/4	1	1	3
1/2	5	3	4
1	10	20	10
2	20	40	40
4	70	70	*50*
8	90	*90*	20
16	*100*	45	5
32	50	10	1

[a] Ratio of carbon concentration to carbon concentration of a 0.1 M dextrose solution. Thus, each of the following solutions has a relative carbon concentration of unity: 0.05 M sucrose, 0.1 M dextrose, 0.2 M glycerine.

[b] Only a few, extremely small tufts of spores produced.

which π is the osmotic value in atmospheres, M is the volume-molecular concentration, R is the constant 0.082, and T is the temperature on the absolute scale (here considered to be 273 plus 21, or 294). The formula thus becomes $\pi = 24.1M$. In making these calculations, osmotic values are thus assumed to be directly proportional to volume-molecular concentrations. It is to be noted that for equivalent carbon concentrations the volume-molecular concentrations, and therefore the osmotic concentrations, are as 0.05:0.10:0.20 or as 0.5:1:2 for sucrose ($C_{12}H_{22}O_{11}$), dextrose ($C_6H_{12}O_6$), and glycerine ($C_3H_5(OH)_3$), respectively.

Examination of table 6 shows at once that the optimum osmotic value for mildew development is 19.28 atmospheres (or 0.8M) for each of the substances, although the relative carbon concentrations of the optimum solutions, as shown in the preceding table, are different—16 for sucrose, 8 for dextrose, and 4 for glycerine.[3] This suggests that the optimum concentration for each substance is limited by the osmotic

TABLE 6

Relation of osmotic concentration of solutions of sucrose, dextrose, and glycerine to development of mildew on leaves of wheat in darkness

OSMOTIC CONCENTRATION, ATMOSPHERES[a]	DEVELOPMENT OF MILDEW		
	Sucrose	Dextrose	Glycerine
0	0[b]	0[b]	0[b]
0.04	1	—	—
0.08	1	1	—
0.15	1	1	1
0.30	1	1	1
0.60	5	1	2
1.21	10	3	3
2.41	20	20	4
4.82	70	40	10
9.64	90	70	40
19.28	*100*	*90*	*50*
38.56	50	45	20
77.12	—	10	5
154.24	—	—	1

[a] Calculated by formula $\pi = 24.1M$, in which π is the osmotic value in atmospheres and M is the volume-molecular concentration.

[b] Only a few, extremely small tufts of spores produced.

properties of its solution, and may be related to serious injury through plasmolysis of leaf cells, to low water-supplying power of the solution, to high vapor-pressure deficit of the atmosphere above the solution, etc. A comparison of tables

[3] The optimum sucrose solution contains 27.37 grams per 100 cc. of solution; the optimum dextrose solution 14.41 grams of the anhydrous sugar; and the optimum glycerine solution, 7.36 grams. These values represent approximately the percentages of solute. For accurate equivalents on the percentage basis (grams of solute per 100 *grams* of solution), the densities of the solutions would have to be known.

5 and 6 indicates that the increase in mildew development, below the optimum, is correlated more closely with the carbon concentration of the solution than with its osmotic concentration. Thus, for the lower concentrations the capacity of the solution to induce the development of the mildew on the wheat leaf seems to be largely determined by carbon concentration and to be nearly the same for different kinds of solutions equivalent in carbon concentration. But as the carbon concentration of a solution of any one of the substances is increased, the increase in effectiveness appears to reach a limit determined by osmotic properties. The optimum solutions of sucrose, dextrose, and glycerine gave indices of mildew development of 100, 90, and 50, respectively. These differences seem to be determined, in part at least, by the fact that without exceeding 19.28 atmospheres a relative carbon concentration of 16 may be obtained with sucrose, while the corresponding carbon concentrations obtainable with dextrose and glycerine are only 8 and 4, respectively.[4]

In general a given osmotic concentration of sucrose induced the production of more mildew than did the same osmotic concentration of dextrose, and the latter had a greater effect than glycerine (table 6). Solutions having the same osmotic value also have the same number of molecules per unit volume, but each molecule of sucrose contains twice as many atoms of carbon as a molecule of dextrose, and a molecule of the latter has twice as many as a molecule of glycerine. Thus, with solutions equivalent in molecular concentration, effectiveness in promoting mildew development appears to be directly related to the amount of carbon contained in each molecule.

The capacity of a solution of an organic substance to increase the susceptibility of the leaf to mildew may be expected to depend upon a very complex set of conditions.

[4] In interpreting these results, it should of course be borne in mind that the optimum concentration for each substance might be determined more precisely by using a series of solutions with smaller gradations in concentration. In the series here employed, each solution has double the concentration of the preceding solution. Although the optimum osmotic concentration, as here determined, is 19.28 atmospheres, it should be recognized that the exact optimum might lie at a somewhat different concentration between 9.64 and 38.56 atmospheres.

The following conditions may be mentioned as important in this connection: (a) the power of the solution to supply organic material to the leaf (depending mainly upon the nature and molecular concentration of the dissolved substance), (b) the capacity of the leaf to absorb the organic substance in question, (c) the possible rate of conduction of the organic substance or its products to the epidermal cells, (d) the capacity of the leaf to transform the substance into materials that can be utilized by the fungus, and (e) the nature and degree of chemical and osmotic effects which the solution exerts upon host and parasite.

Only very small amounts of starch were found in uninfected and infected wheat leaves supplied in the dark with solutions of sucrose, dextrose, or glycerine. Tests were made in the usual way, by placing leaves in boiling water for one minute, then in alcohol until decolorized, and finally in a weak solution of iodine in fifty per cent alcohol, with enough chloral hydrate to nearly saturate the solution. The leaves showed no blue coloration to the naked eye, and microscopic examination revealed only a very small number of starch grains, in the bundle sheaths. Wheat leaves from plants out-of-doors also contained no starch or only a very slight trace. The wheat plant apparently stores soluble carbohydrates as such and does not transform them into starch. Even the amount of soluble carbohydrate accumulated seems to be small under usual conditions with the leaf attached to the plant. Sugar analyses would be instructive in this connection.

The mineral nutrition of these wheat leaves did not appear to be a limiting factor in the ability of the leaves to support mildew in these experiments. Mildew development was found in preliminary tests to be nearly the same on excised leaves supplied with a number of different three-salt solutions containing sugar; and the results seemed to be the same when tap water or distilled water was used in preparing sugar solutions. Since the susceptibility of plants grown for longer periods in solution cultures may be markedly influenced by the composition of the solution (Trelease and Trelease, 1928), it may be expected that leaves in darkness may be found to differ in susceptibility if variations in mineral supply are sufficiently pronounced. The present study suggests, more-

over, that low susceptibility of plants grown in some culture solutions may result from an inhibition of the normal manufacture of carbohydrates in the leaves; this might occur, for example, when the culture solution contained toxic concentrations of salts of the heavy metals or when it contained the usual mineral nutrients in markedly unbalanced proportions.

Chlorophyll disappears rather rapidly from wheat leaves supplied with the various sugars in darkness, so that pronounced chlorosis is evident after from seven to ten days. Differences were observed, however, in the rate of chlorophyll disappearance from leaves receiving the various solutions, the most conspicuous difference being the longer retention of the chlorophyll in leaves supplied with glycerine. The green color also remained longer in leaves that were free from mildew—uninoculated leaves in carbohydrate solutions and inoculated leaves receiving only tap water or distilled water. Thus, mildew infection hastens the disappearance of chlorophyll from the leaf in the dark as well as in the light. Chlorophyll persisted longer in the neighborhood of mildew spore tufts than in other parts of the leaf. This is the so-called green-island phenomenon, widely observed and reported in the literature of the rusts (see especially Rice, 1927). Reed (1904) reported that cells of the infected areas of the rye leaf retained their green color for a longer time than the other cells, while the reverse was true for the blue-grass leaf.

When the spores were scraped from leaves kept in the dark a new tuft of spores developed in one or two days. Spores continued to be produced for more than a week, until the leaves gave every external indication of being dead. Thus, the process appeared to be like that occurring in infected leaves in the greenhouse.

That chlorphyll is unnecessary for the development of mildew in the dark was clearly shown by a test with etiolated leaves, made at the same time as the tests recorded in tables 5 and 6 and with seedlings of the same age but grown in the dark. The leaves lacking chlorophyll were treated in the same manner as the green leaves and were supplied with sucrose and dextrose solutions, each with a relative carbon concentration of 4. Mildew developed as rapidly and as abundantly on these leaves as on those which contained chlorophyll.

INFLUENCE OF CARBOHYDRATE SOLUTIONS UPON SUSCEPTIBILITY OF LEAVES DEPRIVED OF CARBON DIOXIDE

It would be expected from the preceding experiments and from Mains's (1917) study of rusts that wheat leaves deprived of carbon dioxide would not be susceptible to mildew, even in the light, unless a suitable carbon compound were supplied to the leaves. This was readily demonstrated by the test described below.

Wheat plants, about 18 cm. high, were placed in the dark for two days so that most of their surplus carbohydrate food would be exhausted. The plants were then sprayed with distilled water and heavily inoculated with mildew spores. Three leaves were removed and placed with their cut ends in tap water in a small vial, and the vial was suspended in a two-quart Mason jar. A wire passed around the neck of the vial, and a loop in the upper end hung on a hook inserted in a paraffined cork stopper that closed the mouth of the jar. The cork bore a straight calcium-chloride tube with a vial suspended about its lower end. This tube was filled with small pieces of pumice stone. The jar contained tap water to a depth of about 2.5 cm. A second jar was arranged with pieces of potassium hydroxide mixed with pumice in the calcium-chloride tube, and with potassium hydroxide solution (120 grams of KOH in 400 cc. of water) replacing water in the bottom of the jar. A third jar was similar to the second except that a 3 per cent sucrose solution (relative carbon concentration, 1.75) was used instead of tap water in the vial holding the leaves. All three jars were placed in a north window of the laboratory.

The first chamber thus contained ordinary air. The second and third contained air lacking carbon dioxide. The leaves in the first two chambers received tap water, while those in the third chamber were supplied with a carbohydrate solution.

Well developed tufts of mildew spores appeared after five days on the leaves in the first and third jars; no spores were visible on the leaves of the second jar, even after ten days.

This experiment shows that development of mildew spores does not occur on leaves exposed to light and kept in an atmosphere free from carbon dioxide, but that the leaves may be-

come susceptible if supplied with a solution containing a suitable carbon compound.

DISCUSSION

Conditions determining the susceptibility of wheat to mildew. The results of the present study show that the susceptibility of the wheat leaf to a given strain of mildew was promoted by conditions which led to the accumulation of surplus carbohydrate in the leaf. Although it may be inferred that the degree of susceptibility was here controlled by carbohydrate content, sufficient information is not available to show whether the carbohydrates themselves, or whether other substances (proteins, etc.), whose formation is dependent on carbohydrates, are directly influential in determining susceptibility. The term susceptibility is used in a broad sense to denote the summation of the conditions within the host that tend to facilitate injury by the parasite. And the criterion of susceptibility here employed is the relative abundance of mildew spores developed per unit area on a number of different leaves, which had previously been equally inoculated with mildew spores and then kept under conditions tending to assure uniform pathogenicity of the parasite.

It may be expected that many complex conditions operate together in determining the degree of susceptibility of a particular host to a given parasite. The relative quantitative significance of the various component conditions may be very different in different cases. Thus, it is conceivable that morphological conditions, nitrogen content of the host cells, water content, hydrogen-ion concentration, concentration of certain substances that are poisonous to the parasite, kinds and concentrations of carbohydrates, proteins, fats, enzymes, pigments, etc., may each exert a preponderating influence in certain cases. With the general conditions involved in the present study, susceptibility of the wheat leaf to a certain strain of mildew appears to be proportional to the carbohydrate content of the epidermal cells of the host.[5] It therefore

[5] Failure of the host to supply the fungus with adequate food materials seems to be the simplest explanation of the low susceptibility of leaves lacking a carbohydrate excess. Other important features may, of course, be correlated with low food content—substances poisonous to the fungus may be produced most abundantly in host cells inadequately supplied with carbohydrate food,

seems worth while in this connection to summarize briefly the conditions that determine the carbohydrate content of the epidermal cells into which the parasite grows.[6] The carbohydrate content of the epidermal cells at any particular time may be considered to depend upon the following conditions:

I. Past rates and periods of processes tending to increase carbohydrates in epidermal cells, depending upon:
  A. Rates and periods of entrance of carbohydrates into epidermal cells, depending upon:
    a. Carbohydrate content of subepidermal cells, depending upon:
      1. Rates and periods of processes tending to increase carbohydrate in subepidermal cells, depending upon:
        (A) Rates and periods of entrance of carbohydrates from outside the cells (as from endosperm, from other parts of plant, or from carbohydrate solutions supplied to leaf).
        (B) Rates and periods of formation of carbohydrates in these cells:
          (a) By photosynthesis, depending upon:
            (1) Quality and intensity of absorbed light.
            (2) Carbon dioxide absorption.
            (3) Temperature.
            (4) Chlorophyll content.
            (5) Water content.
            (6) Concentrations of products.
            (7) Condition of protoplasm (dependent on the nature of the plant and on the sum total of previous physical and chemical conditions or stimuli).
          (b) By other physiological processes (usually a negligible factor).
      2. Rates and periods of processes tending to decrease carbohydrates in subepidermal cells, depending upon:
        (A) Rates and periods of exit of carbohydrates (by translocation, to epidermal cells, out of leaf, etc.).
        (B) Rates and periods of decomposition of carbohydrates (by respiration, protein formation, assimilation of protoplasm, etc.).

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or such cells may be most readily killed (hyper-sensitive) and thus lead to death of haustoria. Low protein content of the host cells, generally associated with deficient carbohydrate supply, may be an important condition in determining low susceptibility.

[6] It is of course realized that this outline is tentative and incomplete, and that even the relations which the outline attempts to indicate might be shown by a number of other schemes.

b. Rates and periods of movement of carbohydrates from subepidermal to epidermal cells.

B. Rates and periods of formation of carbohydrates within epidermal cells, by photosynthesis in stomatal guard cells and by transformation of various organic compounds in epidermal cells.

II. Past rates and periods of processes tending to decrease carbohydrates in epidermal cells, depending upon:

A. Rates and periods of movement of carbohydrates out of epidermal cells (by movement into other host cells and into fungus haustoria).

B. Rates and periods of decomposition of carbohydrates (by respiration, protein formation, assimilation, etc.).

Absence of disease under conditions of high susceptibility of the host. Since the actual development of disease depends not only upon the susceptibility of the host but also upon the pathogenicity of the parasite, sets of influential conditions may exist in which no development of the disease occurs in spite of high susceptibility of the parasite and heavy inoculation with mildew spores (see discussion by Trelease and Trelease, 1928). This appears to be the explanation of the usual absence of wheat mildew on plants growing out-of-doors in full sunlight.

Duggar (1909) states that wheat under partial shade often is badly infected with powdery mildew, which in the central part of the United States is seldom, if ever, seen in the open. He also says that time and again, in that same region, one may observe that in the case of well-watered lawns the mildew of blue grass abounds in a circle rather sharply limited by the heavier shadow areas of trees. Butler (1918) states that wheat mildew in India has only been seen causing serious damage in half-shaded pot culture experiments.

These general observations were confirmed by tests made during the summer in full sunlight and under deep shade of trees near the Columbia University greenhouses. Inoculated plants kept in the shade always became heavily infected with mildew, while those in the open usually showed only a slight flecking of the epidermis and no development of spore tufts.

It appears probable that direct sunlight increases the rate of photosynthesis and therefore tends to increase the susceptibility of the host to mildew, but intense light seems also to inhibit the pathogenicity of the parasite, by direct

action or because of high evaporation and consequent drying of the mildew conidia and superficial mycelium. Thus, the actual development of the disease may be completely inhibited in spite of the high susceptibility of the host.

Observations on the relation of temperature to mildew development have indicated that the optimum temperature is about 20°C., and that practically no development of mildew occurs at 30°C. It is impossible as yet, however, to state to what degree the checking of the disease by high temperatures depends upon low pathogenicity of the parasite and to what degree it depends upon low susceptibility of the host (the latter possibly associated with low carbohydrate content as the result of high rates of respiration and low rates of photosynthesis). Reed (1916) observed that only very slight infection occurred on plants kept under bell-jars exposed to bright sunlight in a greenhouse that had not been whitewashed. He attributed the low degree of infection to the high temperature within the bell-jar, but he did not determine the relative effects of temperature upon host and upon parasite.

SUMMARY

Wheat plants must be exposed to light in order to render them susceptible to mildew (as indicated by their capacity to support development of mildew and production of spores) under usual conditions. When infected plants were placed in the dark for one or two days and later removed to the light, the incubation period was nearly as short as for plants not put in the dark (about three and one-half days). When similar plants were placed in the dark from three to six days, the incubation period was lengthened by a period which was about two days less than the initial period in darkness. Plants left in the dark for seven or eight days were nearly dead at the end of this time, and no mildew developed on them.

Wheat leaves in darkness were susceptible to mildew and supported an abundance of conidia if they were supplied with a solution containing any one of many carbohydrates or with a solution containing glycerine or mannite. Only a few very small tufts of conidia appeared on similar leaves supplied with tap water containing no carbohydrate.

Chlorophyll is not necessary, since mildew developed

as readily on etiolated leaves in the dark as on green leaves, if a carbohydrate or glycerine was supplied to the leaves.

Salt nutrition was not a limiting factor under the conditions of these tests, since a carbohydrate solution made with distilled water was about as effective as such a solution made with tap water or with a nutrient salt solution.

The capacity of solutions of sucrose, dextrose, and glycerine to render leaves in the dark susceptible to mildew appears to be directly related to the carbon concentration of the solution. Susceptibility increased with increase in concentration until a limit was reached which apparently depends upon the osmotic properties of the solution, this limit being about 19 atmospheres for each of the three substances.

Leaves exposed to light and kept in an atmosphere free from carbon dioxide were not susceptible to mildew unless they were supplied with a carbohydrate solution.

Leaves of very young plants, which were receiving a supply of carbohydrates and other materials from the endosperm, were slightly susceptible to mildew in darkness. Leaves detached from these plants and placed in tap water in darkness were also slightly susceptible.

All of the data secured in the present tests indicate that a relatively large surplus of carbohydrate in the host leaf is necessary for the abundant development of mildew; the supply of carbohydrate must be considerably greater than that required for retention of life by the leaf. Under usual conditions the carbohydrates may be transition products of photosynthesis, but they are not necessarily such products, since cut leaves may be rendered susceptible to mildew if supplied with a solution of glycerine or of any one of many carbohydrates.

The development of the mildew appears to be strictly limited by the life of the host. No tendency was observed for the mycelium to spread in the carbohydrate solution beyond the leaves. The green island phenomenon, moreover, suggests the very intimate and possibly even mutualistic relation between the host and the obligate parasite, and indicates that the development of the parasite is dependent upon the continuance of the host's metabolism.

In the present experiments, as well as in a series of tests

on the influence of mineral nutrition on susceptibility, no evidence was obtained which indicated that starvation or any other form of injury to the host favors the development of the mildew.

Although the present tests emphasize the need of more accurate criteria of health and vigor than are now available, a direct relation between general health or vigor of the wheat leaf and susceptibility to mildew seems to be suggested by these studies dealing with the carbohydrate nutrition of the leaf. That carbohydrates are significant not only as materials for assimilation but as sources of energy in protein synthesis is well established. The known facts and the probable relations of carbohydrates to the essential metabolic processes of both host and parasite point to the general conclusion that conditions which tend to lower the vigor of the host decrease the susceptibility of wheat leaves to mildew and conversely conditions which tend to favor the life processes of the wheat plant increase its susceptibility to mildew. This conclusion is in accord with the results of most workers on parasitic disease in plants and apparently contradicts sweeping statements, found in current treatises on animal pathology, regarding the direct relation of lowered vitality to susceptibility.

COLUMBIA UNIVERSITY
NEW YORK CITY

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New species of fossil plants from the Tertiary shales near De Beque, Colorado

ARTHUR HOLLICK

(WITH PLATE 2)

The three species here described and figured were included in a collection of about forty specimens transmitted to me for identification, in August 1928, by the Department of Public Education of the American Museum of Natural History.

Apparently two different floras were represented in the collection. One, which included about two thirds of the specimens, contained a number of species characteristic of the Florissant lake-bed deposits, such as *Celastrus fraxinifolius* Lesquereux, *Fagopsis longifolia* (Lesquereux) Hollick, *Lomatia* cf. *terminalis* or *tripartita* Lesquereux, *Myrica coloradensis* Knowlton, *Myrica drymeja* (Lesquereux) Knowlton, and *Rhus coriarioides* Lesquereux. These may be inferred to be of Oligocene or Miocene age. The other flora, included in the remainder of the specimens, contained several species typical of the Green River shales, such as *Aralia wyomingensis* Knowlton & Cockerell, *Myrica praedrymeja* Knowlton, and *Quercus castaneopsis* Lesquereux, which are Eocene in age, and others that represented undescribed species. Among the latter were the three that form the subject matter of this paper.

The collection, in its entirety, is recorded as having been made by Mr. Edmund Reynolds, at 'different altitudes', in the Tertiary oil shale beds in the vicinity of De Beque, Colorado. The probability appears to be that specimens from two different geological horizons are included in the collection; that the three specimens here described belong in the older one; and that this one represents the upper part (Bridger formation) of the Green River shales.

If fuller information should be desired in regard to the exact stratigraphic relations of the shales, the subject may be found critically and exhaustively discussed by Dr. F. H. Knowlton, in his 'Revision of the flora of the Green River formation, with descriptions of new species'[1].

[1] U. S. Geol. Survey, Prof. Paper 131-F (Shorter contributions to general geology. 1922), pp. 133–182. *pl. 36-40.* Mar. 30, 1923.

Pontederites thecoides n. sp. Organism apparently representing the remains of a membranous spathe, sheath, or bract-like leaf, 12 or more centimeters in length, expanded at one extremity to a width of about 2 cm., and contracted, for a distance of 3.5 cm. at the opposite extremity, to a width of about .75 cm.; nervation consisting of numerous closely approximated parallel veins, including a major series and an obscurely defined minor series between, the two series connected by numerous cross veinlets that subtend approximately right angles with their supporting veins, forming a fine quadrangular reticulation throughout. Museum New York Bot. Gard. No. $\frac{5\,9}{3}$ (plate 2, fig. 1).

Numerous comparisons were made between this specimen and various parts of a number of existing species of monocotyledonous plants, without, however, arriving at satisfactory conclusions in regard to either its generic relationship or its morphologic status. It may be inferred, however, without question, that it belongs in the Monocotyledoneae, and its general appearance is suggestive of a flattened spathe or floral bract, or a clasping basal leaf or sheath common to certain plants such as are represented in the genus *Musa*, and in the genera *Pontederia*, *Piaropus*, etc., in the Pontederiaceae, and *Peltandra*, *Orontium*, etc., in the Araceae; but which is the distal and which the proximal extremity of the specimen I am unable to determine. The broader, disrupted part may have been spathe-like, originally; and the dark, irregular patches, that are conspicuous features where a portion of the membranous area is missing, are suggestive of some disintegrated enclosed organ, such as a spadix or flower cluster. On the other hand it also presents somewhat the appearance of a basal stem sheath, tubular and clasping below, open and flaring above. In the circumstances any more definite expression of personal opinion would appear to be of little value or interest.

Reference of the species to the genus *Pontederites* Knowlton[2] might, perhaps, be regarded as not entirely justified. The genus was based by the author on a disrupted fragment of what he inferred to be the apical part of a monocotyledonous leaf resembling those of *Pontederia cordata* Linnaeus. His figure shows indications of a midvein, which feature is not ap-

[2] Knowlton, F. H., *op. cit.*, p. 154, *pl. 36, fig. 6.*

parent in our specimen. Otherwise, however, the nervation appears to be mutually identical; and inasmuch as both specimens belong in one and the same geological horizon there would seem to be no inconsistency in relegating them to one and the same genus. They may, in fact, represent different organs of a single species—one a leaf, the other a spathe or sheath.

Odostemon Reynoldsii n. sp. Leaflet lanceolate-ovate in shape, coriaceous, about 5 cm. in length by 2.5 cm. in maximum width, tapering above, rounded below to a broad cuneate base, short petiolate; margin finely denticulate from the widest part of the leaflet upward, entire below; nervation pinnate, craspedodrome; secondary nerves irregularly spaced and disposed, subtending various angles with the midrib, flexed and angled, the angles connected by tertiary cross nervation, with ultimate fine nervilles extending to the marginal denticulations. Mus. New York Bot. Gard. $\frac{5.5}{9a}$ (plate 2, fig. 2).

Practically the only discernible difference between this specimen and many of the leaflets of existing species of *Odostemon* Rafinesque (=*Berberis* Linnaeus, and *Mahonia* Nuttall) is the fine marginal denticulation of the fossil as compared with the prevailingly coarser dentition in most of the existing species. Heterophylly, however, is a well marked character of the genus, and leaflets may be readily selected from individual plants that are strikingly similar to ours in form and in marginal features, especially in specimens of *Odostemon nutkanus* (DC.) Gaines, and *O. pallidus* (Hartweg) Gaines, of western North America.

The texture of our specimen was obviously thick and coriaceous, as indicated by the obscurely defined secondary and tertiary nervation; and the symmetry of shape, as well as the presence of a petiole, would seem to indicate that it was a terminal rather than a lateral leaflet, which latter are prevailingly unsymmetrical and sessile in existing species.

Several fossil species have been described from Tertiary deposits of the western United States, among which may be mentioned *Odostemon simplex* (Newberry) Cockerell (=*Berberis simplex* Newberry[3]) as an example of their general foliar type; but, from the figures, it may be seen that none is likely to be confused with ours.

[3] Newberry, J. S. U. S. Geol. Survey, Mon. vol. 35 (The later extinct floras of North America), p. 97. *pl. 56, fig. 2.* 1898.

The specific designation, *Reynoldsii*, is given in recognition of Mr. Edmund Reynolds, the collector of the specimen.

Staphylea Viridifluminis n. sp. Capsule, flattened, ellipsoidal or obscurely obovate in outline, 4.5 cm. in length by 2.75 cm. in maximum width, pedicillate, membranous and reticulate-veined throughout, apparently 3-celled or -divided, each division rounded proximad and distad, terminating distally in a short awn or bristle, the three divisions compacted proximad, forming a curved-cuneate, apiculate base; sepals inferior, obscurely defined; pedicel about 3 mm. in length. Mus. New York Bot. Gard. No. $\frac{58}{1}$ (plate 2, fig. 3).[5]

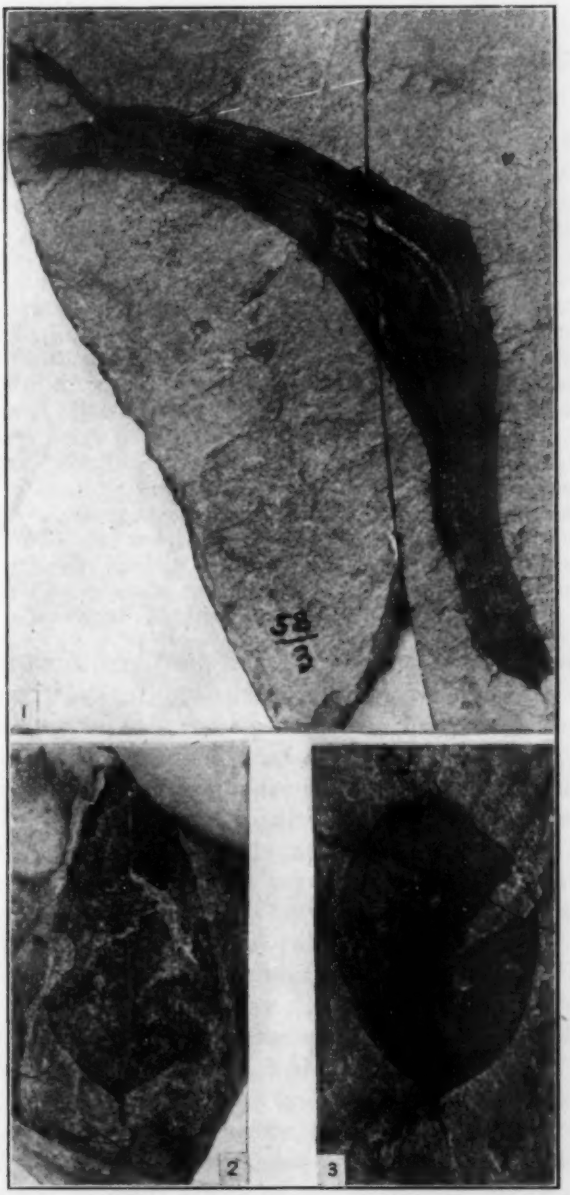
This specimen obviously represents a compressed and ruptured pod or capsule belonging to the genus *Staphylea*, and one so closely comparable with those of the existing *S. trifoliata* Linnaeus as to be impossible of differentiation if, for example, a flattened herbarium specimen is utilized for comparison. Incidentally, also, attention may be called to the rounded and the longitudinal markings in the median part of our specimen, which are strikingly suggestive of impressions of seeds and their accompanying placentae.

Several American Tertiary species of *Staphylea*—based upon the leaflets only—have been described and figured. One of these in particular—*Staphylea acuminata* Lesquereux[4]—from accredited Miocene or Oligocene deposits in Colorado, is satisfactorily identifiable with the genus; and, in as much as its geologic age is relatively close to that of our specimen, it might be of interest to speculate upon the possibility that these leaflets and the capsule now under consideration may be identical specifically, as well as generically. Future collections, in one or another of the deposits in which either the capsule or the leaflets were found, ought to bring such remains to light, associated together.

In conclusion the following quotation from Lesquereux' discussion (*op. cit.*, p. 267) may be of interest: 'The species [*Staphylea acuminata*] is remarkably similar, considering the leaves at least, to the North American *S. trifoliata* Linn.'

[4] Lesquereux, Leo. U. S. Geol. Survey Terr., Rept. vol. 7 (The Tertiary flora), p. 267. *pl. 48, figs. 4, 5.* 1878; *idem*, vol. 8 (The Cretaceous and Tertiary floras), p. 183. *pl. 36, figs. 1–4.* 1883.

[5] Plate 2 from photographs by Henry C. Hartmann.



1. PONTEDERITES THECOIDES
2. ODOSTEMON REYNOLDSII
3. STAPHYLEA VIRIDIFLUMINIS

Studies on the flora of northern South America—XII[1]

H. A. Gleason

Cyphostyleae—a new tribe of Melastomataceae

Stems woody. Leaves 5-pli-nerved. Inflorescence racemose, terminal or axillary. Flowers 5-merous. Hypanthium and calyx densely hirsute, the calyx calyptriform, deciduous at anthesis, entire or separable into five sepals. Petals ample. Torus expanded horizontally even before anthesis, thick and fleshy, bearing the stamens and petals on its distal face, more or less arched over the mouth of the hypanthium. Stamens 5, episepalous in position, the stout filaments strongly incurved at the summit and again recurved to the erect anther; anthers oblong, stout, 2-celled, opening by a lateral pore at the summit of the deep ventral furrow; connective neither prolonged nor appendaged, continued without obvious articulation into the filament. Ovary wholly inferior, 5-celled; ovules numerous, minute, on an elongate placenta which is attached to the axial angle of the loculus by its center only. Style clavate, stout, the summit sharply curved or recurved to the broad truncate stigma. Fruit a capsule, dehiscent by 5 valves. Seeds numerous, straight, the raphe surrounded by a broad fimbriate wing.

The tribe differs from all other melastomes in numerous characters. Calyptriform deciduous calyces are rare in the family, but occur in several genera. An expanded, terminal, pentagonal, fleshy torus is unknown to me elsewhere in the family. Several genera with strongly dimorphic stamens tend to suppress completely the inner circle, as *Monochaetum*, but the condition is comparatively rare, while the shape of the stamens, with their stout anthers set on S-shape filaments, is peculiar to the new tribe. Several genera present anthers with apparently lateral pores, caused by the bending of the anther immediately at the summit, but in the Cyphostyleae the anther is straight and the pore distinctly lateral. In various genera the style is gently curved or more or less sigmoid, but no others have such an abrupt hook at the summit of a clavate style. In no other genera known to me are the placentae attached by their centers only, with their ends extending down and up through the loculus. While capsular fruits are characteristic of eight tribes of the subfamily Melastomeae,

[1] Contributions from The New York Botanical Garden, No. 307.

they proceed almost invariably from ovaries wholly or nearly superior, while here the ovary is completely inferior. Two genera are included:

Inflorescence axillary; calyx separating into distinct sepals before falling; torus sharply pentagonal, the projecting lobes simulating calyx-lobes but opposite the petals; summit of the anther arched over the pore, which is directed basally; summit of the style recurved; leaves strongly anisophyllous ..... *Allomaieta.*

Inflorescence terminal; calyx not separating into distinct sepals; torus round or obtusely pentagonal; summit of the anther not arched over the pore, which is distinctly lateral; summit of the style bent at right angles; leaves of each pair essentially equal in size ..... *Cyphostyla.*

Allomaieta gen. nov.

Characters of the tribe. Stem, leaves, and inflorescence hirsute. Leaves unequal in each pair, the smaller cordate, the larger obovate; petioles short. Inflorescence small, axillary, the branches and short-pedicelled flowers subtended by subulate bracts. Hypanthium campanulate, terminating in the acutely pentagonal torus. Sepals large, erect and connivent before anthesis, soon deciduous. Petals large, obovate, obtuse. Ovary glabrous. Stigma truncate-retuse. Fruit capsular, the hypanthium dehiscent to the middle in five valves. Seeds minute, semiovoid, the raphe surrounded by a broad, deeply fimbriate wing.

Allomaieta grandiflora n. sp. Petioles 5 or 10 mm. long, hirsute like the stem; smaller leaf-blades cordate-ovate, reflexed, 15–30 mm. long, 12–20 mm. wide, obscurely 5-nerved, abruptly acute; larger leaf-blades obovate-oblong, the largest 18 cm. long and 7 cm. wide, acuminate, entire, narrowed from above the middle to a cordate base, the auricles overlapping above the petiole, 5-pli-nerved, the intermediate pair arising 2–3 cm. above the base; midvein densely hirsute above, secondaries prominulous only beneath, ascending at almost right angles, veinlets plane and finely reticulate; inflorescence 5–6-flowered, 2–3 cm. long; bracts 3–4 mm. long; pedicels about 2 mm. long; hypanthium 3 mm. long, obscurely 10-ribbed, densely hirsute; sepals narrowly triangular-lanceolate, 9 mm. long, acuminate, long-hirsute; petals broadly cuneate-obovate, obtuse, glabrous, entire, 22 mm. long; filaments stout, somewhat flattened, erect, about 4.5 mm. long; anthers acute, nearly 2 mm. long; ovary radially 5-ribbed at the summit; style about 5 mm. long; stigma 0.8 mm. in diameter; fruiting hypanthium about 5 mm. long, the valves spreading or somewhat recurved; seeds with semi-ovoid, sharply tuberculate body 0.25–0.4 mm. long, the wing as wide as the seed or somewhat wider.

Type, *Ariste-Joseph 1083*, collected at Paime, Dept. Cundimarca, Colombia, and deposited in the United States National Herbarium as number 1,189,081 (duplicate in the herbarium of the New York Botanical Garden).

The anthers are stout and plump, like those of *Miconia* section *Amblyarrhena*, but differ in their method of dehiscence. Toward the base of the anther, the two pollen-sacs are separated by the usual suture; in the terminal quarter of the anther the sacs are confluent and project ventrally, so that the single pore is hidden beneath this projection and is directed basally. The fruiting hypanthium is only slightly enlarged and at maturity splits from the summit backwards about halfway to the base, along the lines of the sepalar mid-veins. The summit of the capsule of course splits radially at the same time and the dissepiments break from the axis, persisting along the wall of the hypanthium and leaving a free central axis. The minute seeds are semi-ovoid in shape and somewhat pointed. Along the straight side, or raphe, the seed bears a broad, thin, deeply fimbriate membrane surrounding the raphe and large enough to double the size of the seed proper.

Cyphostyla gen. nov.

Characters of the tribe. Inflorescence densely hirsute. Leaves essentially equal, ovate-oblong, on conspicuous petioles. Inflorescence terminal, loosely flowered, with long pedicels, the bracts none or early deciduous. Hypanthium obconic, densely hirsute with reflexed hairs. Sepals erect and united into a conic calyptra, deciduous at anthesis. Petals large purple, triangularly obovate or somewhat retuse. Ovary glabrous. Stigma truncate-retuse.

Leaves ovate-oblong, sharply acuminate ..... *C. hirsuta.*
Leaves oblong, subacuminate to a blunt tip ..... *C. villosa.*

Cyphostyla hirsuta n. sp. Stem, petioles, and inflorescence hirsute with purplish hairs 1–1.5 mm. long; petioles 5–10 mm. long; leaf-blades firm, ovate-oblong, the largest 9 by 3.5 cm., sharply acuminate, entire, appressed-ciliate with stout hairs, rounded at the base, 5-pli-nerved, the secondaries about 2 mm. apart; upper surface pubescent on the veins with short yellowish hairs 0.2 mm. long, hirsute on the surface proper with purplish hairs 1.5–1.7 mm. long; lower surface pale green and softly villous on surface and veinlets with erect whitish hairs 0.5–0.8 mm. long, sparsely hirsute on the primaries with purplish

hairs 1–1.5 mm. long; inflorescence 1–3 cm. long, few-flowered; hypanthium 6 mm. long, 6 mm. in diameter at the summit, fleshy, completely covered with stout, simple, retrorse bristles 3.5 mm. long; calyptra 8 mm. long, hirsute like the hypanthium; petals purple, 2 cm. long and broad; filaments about 5 mm. long; anthers 5 mm. long; style about 9 mm. long.

Type, *Pennell 10,963*, collected at Primavera, Dept. Antioquia, Colombia, alt. 1800—2200 m., 22 Sep. 1922, and deposited in the herbarium of the New York Botanical Garden.

Cyphostyla villosa n. sp. Stem, petioles, and inflorescence pubescent, more densely toward the summit, with brownish papillose hairs 1–1.2 mm. long, the terminal seta soon deciduous; petioles 10–25 mm. long; leaf-blades oblong, thin, the largest 13 by 5 cm., subacuminate to a blunt tip, entire, obtuse at base, 5–pli–nerved, the secondaries 3 mm. apart; upper surface scabrous with short conic projections, many of which are tipped with strigose yellow hairs 1–1.5 mm. long, and villous on the veins; lower surface thinly villous on surface and veins alike with whitish hairs 0.5–1 mm. long; inflorescence 10–15 cm. long, the lower pedicels as much as 3 cm. long and all jointed 5 mm. below the summit; hypanthium 5 mm. long, densely hirsute with reflexed hairs 3 mm. long; calyptra 15 mm. long, hirsute like the hypanthium; petals purple, triangular, slightly retuse, 25 mm. long and broad; filaments 5 mm. long; anthers 3.5 mm. long; style 7 mm. long.

Type, *Toro 1038*, collected at Fredonia, vicinity of Medellin, Dept. Antioquia, Colombia, 30 June 1928, and deposited in the herbarium of the New York Botanical Garden. The mature fruit and seeds of both species *Cyphostyla* are as yet unknown.

Hypericum, subsection Eubrathys, in northwestern South America

The genus *Hypericum* is represented in northern South America only by the section *Brathys*. Of the numerous species in the region, the most striking in appearance are the shrubs of the subsection *Eubrathys*, characterized by their freely branching, usually bushy habit and their small, crowded, frequently imbricate leaves. Considerable confusion has developed in the identification of the material of this subsection in American herbaria, due primarily to the lack of any adequate monographic treatment since 1862, when Triana and Planchon dis-

cussed the species of Colombia. Keller supplied a key to the species of the group in 1908, unaccompanied by descriptions and citations, except for a few new forms therein proposed, and almost the same arrangement reappeared in the second edition of the Natürlichen Pflanzenfamilien. As a further contribution to our knowledge of the group, the following key is offered, based primarily on the large amount of material in the herbarium of the New York Botanical Garden, which has been compared with the equally copious material at Kew and Berlin. It has been possible to see either types or authentic material of nearly every published species.

All members of the group agree in the general structure of the flower, exhibiting lanceolate to ovate or obovate, rather stiff and erect, green sepals, strongly inequilateral, oblong to obovate-rotund, yellow petals, numerous (12-120 or more) distinct stamens, and three (rarely four or five) styles, which are connate only in the single species *H. aciculare* HBK., of Ecuador. I have not dissected this species and it is omitted in the key. Differences in the shape of the petals exist among the species, but their shape can not often be ascertained with accuracy, even after careful dissection. Diagnostic characters lie chiefly in the number of stamens and in the dimensions and relative proportions of the different floral parts. In these features each species shows a high degree of constancy. The floral structures must always be supplemented by the foliar characters, and the leaves vary from narrowly linear to broadly ovate or obovate, from thin to stoutly ellipsoid, and from involute to flat or revolute. In the key below, the shape and size of the leaf and the size of the petals, number of stamens, and proportions of styles and ovary is given for each species. A variation of about a fifth in dimensions may be expected in any series of specimens, so that a species stated to have petals 10 mm. long will probably show extremes of 8 and 12 mm.

Group 1. Leaves only 2–6 mm. long.

Petals more than 10 mm. long; stamens about 100; styles 5–8 mm. long and 2–3 times as long as the ovary.

Leaves flat.

Leaves recurved-spreading, crisped on the margin when dry, averaging 2–3 mm. long..... *H. thuyoides* HBK.

Leaves strictly erect, thick, firm, or subfleshy.

Leaves rather remote, ovate, flat, averaging 4 mm. long
.....*H. Hartwegi* Benth.
Leaves imbricate, narrowly ovate, involute or boat-shaped, those of the flowering branches only about 2 mm. long
.....*H. myricariifolium* Hieron.
Leaves linear, involute.....*H. laricifolium* Juss.
Petals 5–9 mm. long; stamens few or many; styles 1.5–4.5 mm. long.
Leaves thick and fleshy, somewhat boat-shaped, linear to oblanceolate, erect, longer than the internodes, 1.5–2.5 mm. long; stamens about 60; styles twice as long as the ovary.....*H. Lindenii* Keller.
Leaves linear, involute, acerose.
Stamens about 35; styles 1.5 mm. long, twice as long as the ovary
.....*H. bryoides* Gleason.
Stamens about 90; styles 4.3 mm. long; ovary 3.5 mm. long
.....*H. laricoides* Gleason.
Leaves flat, strictly erect and imbricate, somewhat fleshy or firm, ovate, about 5 by 3 mm.; stamens about 45; styles about 3 mm. long, twice as long as the ovary.....*H. quitense* Keller.
Leaves flat, thin, spreading, conspicuously exposing the quadrangular internodes, mostly 3–6 mm. long.
Stamens 20–30; styles 2mm., ovary 1.4 mm. long
.....*H. loxense* Benth.
Stamens about 100; styles 4.5 mm., ovary 1.5 mm. long
.....*H. carinosum* Keller.

Group 2. Leaves revolute.

Stamens about 100; petals 13 mm. long; styles 8 mm. long, three times as long as the ovary; leaves linear, 8–10 mm. long
.....*H. chamaemyrtus* Tr. & Pl.
Stamens about 25; petals 8–10 mm. long; styles 0.5 mm. long, less than half as long as the ovary; leaves lanceolate, 1 cm. long
.....*H. gnidioides* Seemann.

Group 3. Leaves narrowly linear, acerose, involute, about 10 mm. long.

Stamens 12–40; petals 4–7 mm. long.
Styles normally 5, about equaling the ovary...*H. Brathys* Lam.
Styles 3, much shorter than the ovary.....*H. strictum* HBK.
Stamens 60–120; styles about equaling the ovary.
Petals about 7mm., filaments 4 mm., styles 1.9 mm. long
.....*H. Holtoni* Gleason.
Petals 10–14 mm., filaments 6 mm., styles 4–4.5 mm. long.
Leaves acicular, about 1mm. wide, closely involute
.....*H. struthiolaefolium* Juss.
Leaves linear, 2–4 mm. wide, scarcely involute
.....*H. Weberbaueri* Keller.

Group 4. Leaves flat, 6–25 mm. long.

Stenophyllous species: leaves 2.5–4 mm. wide and 4–8 times as long.

Styles 1.5–2 mm. long, about half as long as the ovary.
Stamens 20–30; styles 4; petals about 5 mm. long
.....*H. Jahnii* Keller.
Stamens about 50; styles 3; petals about 10 mm. long
.....*H. lancifolium* Gleason.
Styles a third to a half longer than the ovary.
Petals 7 mm., sepals 6 mm. long; stamens 40–50.
Flowers solitary at the tips of the branches
.....*H. thymifolium* HBK.
Flowers in small clusters.....*H. Jussiaei* Pl. & Lind.
Petals about 10 mm. long; sepals 9 mm. long; stamens 60–70
.....*H. Weberbaueri* Keller.
Styles 2.5–3 times as long as the ovary; stamens 80–100.
Petals 6–7 mm. long; styles 4.5 mm. long..*H. carinosum* Keller.
Petals 14 mm. long; styles 8.5 mm. long...*H. Phellos* Gleason.
Platyphyllous species: leaves 3–10 mm. wide and 2–3 times as long, or even proportionately broader; petals 10–14 mm. long.
Styles 2–3 times as long as the ovary; stamens 80–120.
Leaves elliptic, sharply acute.....*H. stenopetalum* Turcz.
Leaves obovate, obtuse or rounded.....*H. platyphyllum* Gleason.
Styles equalling or somewhat longer than the ovary; stamens 40–55.
Leaves obtuse or rounded, elliptic.....*H. mexicanum* L.
Leaves sharply acute.
Leaves ovate-lanceolate, falcate, glaucous, flabellately nerved
.....*H. pimelioides* Pl. & Lind.
Leaves elliptic, straight, green, 1-nerved.*H. caracasanum* Willd.

Hypericum bryoides n. sp. Stems freely and cespitosely branched, forming compact bushes about 1 dm. high; terminal branches 1–3 cm. long, erect, densely leafy, with internodes 0.5 mm. long; leaves crowded, imbricate and beautifully decussate, ascending, sessile, lance-subulate, rather thin, involute or boat-shaped, channeled on the lower side along the midvein, conspicuously punctate in two longitudinal rows, 2.5–3 mm. long, 0.5 mm. wide before unrolling; flowers solitary on very short pedicels at the summit of the branches; sepals ovate-lanceolate, 3–3.5 mm. long, 0.9–1.1 mm. wide, obscurely 3-nerved; petals obliquely obovate, 3.5–4 mm. long, 2–2.2 mm. wide, not apiculate; stamens about 36, very irregular in length, the longest 3 mm.; ovary ovoid, 0.8 mm. long; styles 3, stout, erect, 1.5 mm. long.

Type, *Killip & Smith 19,533*, collected on the western slope of the Páramo de Santurbán, Dept. Santander, Colombia, alt. 3000 m., 18 Feb. 1927, and deposited in the herbarium of the New York Botanical Garden; also *Killip & Smith 18,631*, from Páramo de Romeral, Dept. Norte de Santander, alt. 3800—4200 m.

Hypericum laricoides n. sp. Freely branched; stems naked below with exfoliating bark; internodes 3–4 mm. long on the principal branches, their leaves linear or linear-lanceolate, acerose, involute, 5–6 mm. long; microphyllous axillary shoots freely developed, rarely exceeding the subtending leaves and bearing imbricate leaves 3–4 mm. long; flowers solitary, terminating elongated microphyllous shoots, the pedicels 1–2 mm. long; sepals ovate-lanceolate, acuminate, 6 mm. long, faintly 5–nerved; petals obliquely obovate, 9 mm. long; stamens about 90, all separate, 4.5 mm. long; ovary ovoid, 3.5 mm. long; styles 3, separate, 4.3 mm. long.

Type, *Pittier 12,713*, collected on the Páramos de Timote, Merida, Venezuela, alt. 3800—4200 m., where it forms extensive colonies, 24 Jan. 1928, and deposited in the United States National Herbarium. The plant has the aspect of *H. laricifolium*, but differs in its acerose leaves, somewhat smaller flowers, and much shorter styles.

HYPERICUM STRICTUM HBK. The species is common and widely variable. In its typical form it does not extend north of Bogota, but varieties occur in Santander and Norte de Santander.

Hypericum strictum **compactum** (Tr. & Pl.) new comb. (*H. struthiolaefolium compactum* Tr. & Pl.). Low cespitose shrub 1–3 dm. high; stems more or less crooked, spreading, freely and compactly branched, the branches short.

Páramos de Santurbán and Romeral, Santander and Norte de Santander. Although differing remarkably from the species in its general appearance, the flowers maintain the typical structure precisely.

Hypericum strictum **reductum** n. var. Floral parts all much smaller then the type, the petals 4 mm., sepals 2.7 mm., stamens about 15, the longest only 3 mm., ovary 2.1 mm., styles 1.6 mm.

Type, *Killip & Smith 19,534*, collected on the western slope of the Páramo de Santurban, toward Tona, Santander, Colombia, alt. 3000 m., 18 Feb. 1927, and deposited in the herbarium of the New York Botanical Garden.

Hypericum Holtoni n. sp. Stems freely and compactly branched, obscurely quadrangular, the principal internodes 5–7 mm. long; leaf-bearing branches rather crowded, the in-

ternodes 2–3 mm. long; leaves recurved-ascending, narrowly linear, 10–12 mm. long, involute, pungently pointed; flowers solitary, terminating the numerous short lateral branches; sepals lanceolate, acuminate, 5.5 mm. long; petals oblong, 7 mm. long, 2.4 mm. wide; stamens about 65, 3.7—4.3mm. long; ovary 2.4 mm. long; styles 4(!), 1.9 mm. long.

Type, *Holton 787*, collected 'in montibus juxta Bogotam', Colombia, 10 Nov. 1852, and deposited in the herbarium of Columbia University at the New York Botanical Garden. With the general habit and appearance of *H. Brathys* Lam., its flower-parts are regularly larger and the stamens more numerous. It also resembles *H. strictum compactum* in appearance, but differs in the size of the flowers and number of stamens.

HYPERICUM STRUTHIOLAEFOLIUM Juss. Material has been seen only from Ecuador and farther south; numerous Colombian specimens referred here are mostly *H. strictum HBK.* or *H. Brathys* Lam.

Hypericum lancifolium n. sp. Suffruticose, the older stems invested with minute leaf-bases, the internodes 2–4 mm. long; leaves ascending, sessile, somewhat appressed at base, narrowly linear, 10–12 mm. long, 1.5–2 mm. wide, sharply acuminate; flowers few, solitary at the end of the branches, on pedicels 2–4 mm. long; sepals lanceolate, 1.8–2 mm. wide, 8.5 mm. long; petals narrowly obovate, about 10 mm. long; stamens about 50, 4.3 mm. long; styles 3, 2 mm. long, about half as long as the ovary.

Type, *Killip & Smith 17,138*, collected on open bank, vicinity of La Baja, Dept. Santander, Colombia, alt. 2200—2600 m., 14—28 Jan. 1927,and deposited in the herbarium of the New York Botanical Garden. It is nearly related to *H. Jahnii* Keller, and differs in its three styles, larger petals, and more numerous stamens.

HYPERICUM WEBERBAUERI Keller. Weberbauer's original collection is from Peru. *Pennell 4783*, from Bolivar, Colombia, agrees with the type in all except a few trifling matters of dimensions. I also refer here *Killip & Smith 18,187* and *18,205*, from Páramo de las Puentes, Santander, in which the flowers are somewhat larger than in the type and the persistent leaf-bases are much more conspicuous.

Hypericum Phellos n. sp. Shrub 3–4 mm. high, freely branched above, the bark of the leafless branches conspicuously exfoliating, principal internodes about 1 cm. long, the upper ones 4-angled and marked with 4 rows of conspicuous rounded corky protuberances; microphyllous axillary shoots freely developed and often flowering; principal leaves widely spreading, bright green, sessile, oblong-oblanceolate, 10 mm. long, 3 mm. wide, acute, cuneate to the base, flat, sparsely and inconspicuously punctate, 1-nerved, with a few faint lateral nerves visible on the lower side; flowers solitary, terminal, on pedicels about 3 mm. long; sepals ovate-lanceolate, 6 mm. long, longitudinally veined; petals obliquely obovate, about 13 mm. long; stamens about 100, 5–6 mm. long; ovary ovoid, 3.5 mm. long; styles 3, separate, 8.5 mm. long.

Type, *Killip & Smith 18,199*, collected on Páramo de las Puentes, above La Baja, Dept. Santander, Colombia, alt. 3700—3800 m., 25 Jan. 1927, and deposited in the herbarium of the New York Botanical Garden. Other specimens by the same collectors are *15,650* and *17,727*. *H. Phellos* has a general similarity to *H. Jussiaei* Pl. & Lind. and *H. thymifolium* HBK., but is distinguished by its larger petals, longer styles, and more numerous stamens, as well as by the remarkable development of cork along the younger internodes. These protuberances become flattened out on the older twigs and finally exfoliate and disappear.

Hypericum platyphyllum n. sp. Stems woody, stout and crooked, 5–15 dm. high, freely branched above, leafy only on the smaller branches, the leaves often persisting below as appressed scales; principal internodes only 1 mm. long; leaves decussate, spreading at an angle of about 60°, densely imbricate, coriaceous, pale-green, oblong-obovate, 6 mm. long, 3 mm. wide, obtuse or rounded, cuneate to the base, the upper surface freely, the lower sparsely punctate, a few irregular lateral veins visible on the lower side; flowers solitary, terminal, nearly sessile; sepals oblong-obovate, 5.7–7 mm. long, 2–2.4 mm. wide, inconspicuously longitudinally nerved; petals obliquely obovate, about 14 mm. long; stamens 80 or more, about 7.5 mm. long; ovary ovoid, 2.5 mm. long; styles 3, separate, divergent, 5 mm. long.

Type, *Killip & Smith 18,626*, collected on the Páramo de Romeral, Norte de Santander, alt. 3800–4200 m., 30 Jan. 1927, and deposited in the herbarium of the New York Botanical Garden. Other specimens agreeing with the type are

Killip & Smith 18,559 from the same páramo and *17,496* and *17,515* from Páramo de Santurbán. Their number *15,616*, Páramo de las Vegas, has less crowded leaves 10 by 5 mm.; *18,580*, Páramo de Romeral, has narrower, subacute leaves on longer internodes, frequently with microphyllous axillary shoots, and is referred here with hesitation. *H. platyphyllum* resembles *H. mexicanum* L. in general habit, but differs in its smaller leaves, longer and more numerous stamens, proportionately longer styles, stout crooked stems, persistent leaves, and absence of persistent petiolar scars.

The genus Maripa

The genus was founded by Aublet in 1775, with the single species *Maripa scandens*. Earlier in the same volume he also founded the genus *Mouroucoa*, with the one species *M. violacea*. The latter is now generally recognized as a *Maripa*, and its priority of position led Kuntze to transfer to it all the later species of *Maripa*. Both of Aublet's genera are illustrated in his usual style, and these plates become of the greatest value in associating his names with current herbarium material, since the types are now practically worthless. The obvious points of difference are the large flowers, conic ovary, and long filaments in *Mouroucoa*, in contrast with the small flowers, ovoid ovary, and short filaments of *Maripa*.

The further growth of the genus is shown below.

1818. *M. erecta* G. F. W. Meyer, Prim. Fl. Esseq. 115. British Guiana.
1845. *M. glabra* Choisy, DC., Prodr. **9**: 327. French Guiana.
1846. *M. densiflora* Benth., Hook. London Jn. Bot. **5**: 351. British Guiana.
1869. *M. passifloroides* Benth., in Mart. Fl. Bras. **7**: 207. Alto Amazonas.
M. cayennensis Meissn., op. cit. 208. French Guiana.
M. axilliflora Mart., op. cit. 208. Eastern Peru.
M. cordifolia Klotzsch, op. cit. 209. British Guiana.
1881. *M. nicaraguensis* Hemsl., Biol. Centr. Am. **2**: 382. Central America.
M. panamensis Hemsl., l. c. Panama.
1891. *M. paniculata* Barb. Rodr., Vellosia *ed. 2*. **1**: 59. Brazil.
1892. *M. longifolia* Sagot, in Hallier, Engl. Jahrb. **16**: 525. French Guiana.
1920. *M. scandens argentea* Benoist, Bull. Mus. Hist. Nat. Paris **26**: 560. French Guiana.
1920. *M. repens* Rusby, Descr. S. Am. Pl. 103. Venezuela.
1922. *M. reticulata* Ducke, Arch. Jard. Bot. Rio Janeiro **3**: 248. Brazil.
M. tenuis Ducke, op. cit. 249. Brazil.
1925. *M. scandens albicans* Ducke, op. cit. **4**: 170. Brazil.

Maripa villosa Spreng., *M. spectabilis* Choisy, and *M. acuminata* Rusby are excluded from the genus.

The determination of the application of the older names to current herbarium material is a matter of some difficulty *Mouroucoa violacea* Aubl. has very large flowers and elongate filaments: in these respects it suggests *Maripa passifloroides* Benth., as Sagot suggested on the label of his own specimen. I agree with Sagot in this belief, but do not consider it advisable to resurrect a specific name which has been in disuse for so long a time, unless on the most positive evidence. *M. scandens* Aubl. is characterized by the author as having a cinereous calyx and filaments about as long as the anthers. But one species from the Guianas presents this combination and it is quite probable that the name rightfully belongs here. But Aublet's illustrations are notoriously inaccurate and his descriptions usually omit or neglect the characters now known to be of chief taxonomic value, so that we have no positive proof of the application of his name to this or to any other species. Meissner applied the name to a plant with long filaments, common in French Guiana, and I believe we had better give his opinion the benefit of all possible doubt. *M. erecta* Meyer was based on a plant described by Rodschied as an 'arbor alta elegans,' and this statement has been accepted and continued by recent authors. There is not the slightest reason to believe that *Maripa* is ever arborescent, or that it ever fails to climb unless forced into a trailing habit by lack of proper support. I have accepted Meissner's reference of *Wullschlaegel 821* to this species and have accordingly considered it a synonym of *scandens*. *M. cayennensis* Meissn. appears to be the same. The types of the remaining species of northern South America have been examined.

Corolla deeply 5-fid, the lobes not connected by membranous plaits, 13.5 mm. long over all; filaments dilated at base into flat ciliate triangular appendages 1.6–1.9 mm. wide and 2.4 mm. long, the actual filament inserted on the back just below the summit of the appendage; flowers in axillary racemes; leaves cuneate at base.....1. *M. axilliflora.*

Corolla-lobes connected by membranous plaits; flowers in terminal panicles. Expanded corollas 55–65 mm. long, of which the actual tube consititutes about a fourth; filaments 19–20 mm. long, the flattened base triangular, 5–6 mm. long, 2 mm. wide, glandular-ciliate; summit of filament sparsely glandular; anthers 9–10 mm. long.....2. *M. passifloroides.*

Expanded corollas 30–45 mm. long, of which the actual tube constitutes about a half; filaments 9–14 mm. long, the summit glabrous, the expanded basal portion pubescent or glandular throughout; ovary cylindric or conic.

Sepals ovate to rotund, even the inner three about as wide as long, the outer two glabrous or nearly so.

Filaments sharply incurved 1 mm. below the summit and again recurved at the base of the anther, the latter erect and connivent around the style just below the stigma; expanded base of the filaments 1.4 mm. long and densely villous ..... 3. *M. panamensis.*

Filaments erect, straight or essentially so, the expanded base crisp-pubescent.

Filaments abruptly dilated below into a flat, triangular base 5 mm. long, 1.3 mm. wide, and densely short-pubescent ..... 4. *M. nicaraguensis.*

Filaments stout, subulate, 1.3–1.5 mm. in diameter at base, gradually tapering to the summit, the basal 5 mm. longitudinally grooved on the inner face and pubescent with short stout hairs ..... 5. *M. colombiana.*

Sepals rotund to transversely oblong, the inner three much wider than long, the outer two densely sericeous ..... 6. *M. scandens.*

Expanded corollas mostly less than 25 mm. long, of which the actual tube constitutes about half; filaments 2.5–8 mm. long; inner three sepals not more than 7 mm. wide; ovary subglobose to ovoid or short-cylindric.

Outer two sepals densely sericeous; filaments 4–6 mm. long (or rarely a trifle longer), glandular on the triangular base; ovary short-ovoid, glabrous ..... 7. *M. cordifolia.*

Outer sepals glabrous, but covered wtih minute shining resinous particles.

Filaments about 4.3 mm. long, the expanded base glandular-pubescent with hairs about 0.2 mm. long; ovary short-ovoid, densely villous at the summit ..... 8. *M. densiflora.*

Filaments about 8 mm. long, the expanded base densely villous with minutely glandular crooked hairs 0.5–0.8 mm. long; ovary short-cylindric, glabrous ..... 9. *M. repens.*

Outer sepals glabrous; filaments 2.5 mm. long, the expanded base glandular-ciliate; ovary stoutly ellipsoid, glabrous ..... 10. *M. glabra.*

Flowers unknown ..... 11. *M. longifolia.*

1. MARIPA MAXILLIFLORA Mart. Tarapoto, Peru: Spruce 4230 (type). The original description is adequate and is accompanied by an accurate plate.

2. MARIPA PASSIFLOROIDES Benth. (*Mouroucoa violacea* Aubl.?) Alto Amazonas: *Spruce 1419* (type); British Guiana:

Hohenkerk 713; French Guiana: *Sagot 1160.* Meissner's plate in Flora Brasiliensis indicates a deeply 5-fid corolla, which is not in accordance with the facts. It is distinguished even in foliage by the reticulate venation on the upper leaf-surface.

3. MARIPA PANAMENSIS Hemsl. Panama: *Fendler 255* (type), *Williams 985, Pittier 3994, 5489.* The fruit is ellipsoid, 3 cm. long, longitudinally ribbed, and sharply cuspidate.

4. MARIPA NICARAGUENSIS Hemsl. Nicaragua: *Tate 245, 418* (type); Honduras: *Wilson 633.*

5. **Maripa colombiana** n. sp. Branches flexuous, the flowering stems erect, stout, irregularly angular, becoming furfuraceous-puberulent in the inflorescence; panicle or raceme apparently 1–2 dm. long, the lateral peduncles 2–3 cm. long, jointed in the middle, and bearing one or two flowers; outer sepals leathery, thinner at the margin, subrotund, 8 mm. long, 8.5 mm. wide, glabrous, inner sepals leathery, thinner at the margin, subrotund, 8.3 mm. long, 8.6 mm. wide; corolla 40 mm. long, the tube 22 mm. long and glabrous, the lobes lanceolate, 18 mm. long, densely sericeous with short hairs, the plaits glabrous; stamens attached 4.5 mm. above the corolla-base; filaments straight, subulate, nearly terete, 11.6 mm. long, gradually tapering to the apex, 1.3–1.5 mm. in diameter below, the basal 5 mm. longitudinally grooved on the inner face and densely pubescent with short, stout, simple, rather crooked hairs; anthers 7.5 mm. long; ovary cylindric, acuminate, 5 mm. long, 2 mm. in diameter, glabrous; style 13.5 mm. long.

Type, *André 2355*, collected near Salento, Dept. El Cauca, Colombia, 13 Mar. 1876, and deposited in the herbarium of the Royal Botanic Gardens at Kew. Mature foliage leaves are not present on the specmen.

6. MARIPA SCANDENS Aubl. (*M. erecta* Meyer, *M. cayennensis* Meissn.). British Guiana: *Hancock 96, Schomburgk 110, Jennman 4874, De La Cruz 1372, 1538, 2837, 4483, Persaud 123;* Surinam: *Hostmann 1251, Wullschlaegel 821;* French Guiana: *Sagot 379, Melinon 378* (1877), (1863), (1864).

7. MARIPA CORDIFOLIA Klotzsch. British Guiana: Parker, *Schomburgk 1469 B.* (type), *Im Thurn, Jenman 20, 695, 2499, 2500, De La Cruz 2515, 2635, 2811, 4412, Lang 64.*

8. MARIPA DENSIFLORA Benth. Alto Amazonas: *Spruce 1928;* British Guiana: *Schomburgk 232.5* (type).

9. MARIPA REPENS Rusby. Venezuela: *Rusby & Squires* (type).

10. MARIPA GLABRA Choisy. French Guiana: *Sagot 1398*, *Melinon 141* (1854), *523* (1864), (1864).

11. MARIPA LONGIFOLIA Sagot. It is possible that Hallier was unaware that his recognition and brief mention of Sagot's manuscript name was valid publication of a new species. It is apparently based on *Sagot 1201*, which bears Sagots's name in his own hand, accompanied with the note 'affinis Maripae guianensi (syn. M. scandente) a quo foliis statim diagnoscitur.' The leaves are elongate oblong, 14–18 cm. long, 4–5.5 cm. wide, acuminate to a falcate apex, cuneate to an acute base, conspicuously veined. The fruit is pyriform, 2 cm. long, and obtuse.

A RARE UTRICULARIA FROM BRITISH GUIANA

UTRICULARIA BENJAMINIANA Oliver, Jour. Linn. Soc. **4**: 176. 1860.

Akentra inflata Benj. Linnaea **20**: 319. 1847.

Utricularia puberula Klotzsch, Schomburgk, Reisen in Brit.-Guiana **3**: 1159. 1848. *Nomen nudum.*

Utricularia inflata (Benj.) Pulle, Enum. Vasc. Pl. Surinam 419. 1906.

This rare species has been collected but four times, by Melinon and by Le Prieur and Sagot in French Guiana, by Hostmann (no. *85*) in Surinam, and recently by La Cruz (no. *4514*) in British Guiana. Benjamin mistook the large spur for the lower lip and regarded the real lower lip as the upper; this suggested the generic name *Akentra*. Oliver, examining the same collection of Hostmann rectified the error, but failed to discover the upper lip. Klotzsch's name was never properly published, but its application is shown by the appearance of this name in his hand on a sheet of Hostmann in the Berlin herbarium. Pulle's combination is of course antedated by *U. inflata* Walt. The ample material in the La Cruz collection permits the completion of the description and the provision of more exact measurements.

Lower part of the flowering branches densely tomentose, bearing a whorl of 4–7 ampullae; ampullae 1–2 cm. long, narrowly fusiform, pubescent, bearing filiform, repeatedly branched, pubescent leaves at and near their apices; peduncle glabrous, 10–15 cm. high; inflorescence many-flowered, racemose,

the internodes elongating during and after anthesis to as much as 12 mm.; bracts solitary, scarious, broadly ovate, 0.7–0.9 mm. long, acuminate, slightly saccate at the broadly sessile base; pedicels glabrous, filiform, ultimately 2.5 mm. long; sepals 2, distinct, 0.9 mm. long, the adaxial broadly obovate, the abaxial almost round; corolla divided almost to the base into two very unequal lobes; upper lip erect in bud, nearly straight, 3.2 mm. long, 2 mm. wide at base, bilobed to the middle; lobes broadly semi-ovate, 1.2 mm. wide at base, the upper margins nearly straight and connivent, obtuse; lower lip 6.7 mm. wide, 5.9 mm. long, broadly rounded, abruptly spreading above the very short contracted base, palate none, but the center of the lip somewhat elevated around the opening into spur, which is 2.7 mm. long and about 1 mm. wide; spur directed forward at an angle of about 30° from the lower lip, 10 mm. long, obtusely ellipsoid, 3.3 mm. in diameter, slightly laterally flattened, slightly bilobed at apex along the median line; filaments nearly straight, 0.7–0.8 mm. long, flat, scarious-winged; anthers nearly hemispheric, 0.5 mm. in diameter; ovary globose-ovoid.

INDEX TO AMERICAN BOTANICAL LITERATURE

1926-1928

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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